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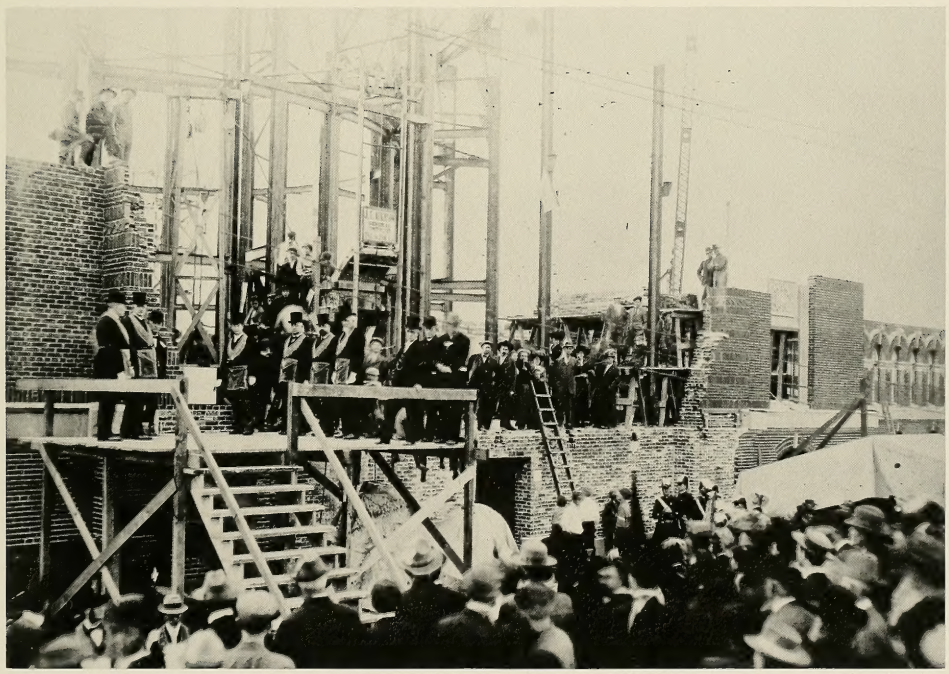

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Academy Centennial 1891–1991

Gretchen Sibley

Southern California Academy of Sciences, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007

A New Scientific Association

For one hundred years the Southern California Academy of Sciences has been an important part of the scientific program of Southern California. While scientific academies were well established in the eastern United States, interest was slow in developing in the west. On 6 November 1891, a group of people interested in science gathered in the parlors of the Hotel Lindley in Los Angeles to organize an association for the promotion of all branches of natural history. Members suggested the name, Southern California Science Association, which was retained for several years. No records remain of those involved, but the following were either at the birth of the young association or carried it through its early faltering steps:

M. H. Alter, optometrist
Bernhard R. Baumgardt, printer and lecturer
D. W. Coquillett, entomologist
Anstruther Davidson, M. D. and botanist
Melville Dozier
Mary E. Hart
John Daggett Hooker
E. W. Jones
Samuel H. Keese, electrical engineer
Abbot Kinney
William H. Knight, journalist
William Lundberg, electrical engineer
J. C. Nevin, retired missionary and botanist
C. R. Orcutt, geologist
George W. Parsons, geologist
Thomas Shooter
William A. Spalding, journalist
William Lord Watts, geologist
M. F. Woodward, judge

A permanent organization was officially established on 16 November 1891 at the Chamber of Commerce Hall. Elected officers were Dr. M. H. Alter, president; Mrs. Mary E. Hart, secretary; and Professor William Lundberg, treasurer. By the end of the year the constitution had been prepared and published. In it the purpose of the organization was delineated: ". . . to secure a more frequent interchange of thoughts and opinions among those who devote themselves to Scientific and Natural History studies; to elicit and diffuse a taste for such studies where it is yet unformed; and to afford increased facilities for its extension where it already exists."

Regular meetings were set for the second Tuesday of each month at 8 p.m. in the Chamber of Commerce Hall at 110 Main Street, Los Angeles. By the end of the first year there were seventy members.

A few "excursions" were planned in the early years. In May 1898 members enjoyed an all-day trip to Mt. Lowe. Abbott Kinney, an academy member who

was the founder of the city of Venice, California, invited academy members for a tour of the amusement center after a scientific meeting held in the city.

Early programs presented at the meetings indicate the wide interests of the members. Some of the subjects were: Meteorology, Shells of Our Pacific Shore, Ducks of Southern California and Their Migration, The Eucalyptus, Spectrum Analysis, Prof. Roentgen's X-Rays, Notes on the Los Angeles and Sespe Oil Fields, Early Man in Europe, Jupiter, Travels on the Continent, and Owens River Aqueduct.

Incorporation

On 12 May 1896, a constitutional change created a new name for the association: The Southern California Academy of Sciences. While a committee had been appointed to work on incorporation, the job was not completed until 17 May 1907. 185 members signed the papers. At that time the treasury contained $68.73 but in 1910 an endowment fund was established provided by life memberships and donations. The largest donation was $10,000 from the Bancroft Etz Bateman estate bringing the total to $22,366.00 in 1917. From 1906 to 1928, Samuel J. Keese served as treasurer and built a sound financial foundation with his shrewd investment program for the Academy. This program has continued to the present under the fine work of a number of treasurers.

Many members were outstanding citizens of the area who contributed to the strength and fine organization of the Academy. Holdridge O. Collins, a meticulous recorder, added poetry to the Bulletin and musical programs to the meetings. Dr. John Adams Comstock was curator of entomology at the Southwest Museum, later moved to the new Museum of History, Science, and Art and was a co-director for a short period. Frank Daggett was the first director of the Museum of History, Science, and Art. John Daggett Hooker achieved international fame as a contributor of the mirror for the 100 inch reflecting telescope for the Mount Wilson Observatory. William K. Knight became a well-known journalist, providing up-to-date scientific information to the press. Another outstanding member was the botanist, Theodore Payne, who preserved the natural plants of the area. He established a garden of California wild flowers and shrubs in the southeast corner of Exposition Park in 1915. Dr. Hector Alliot, archaeologist, was the first director of the Southwest Museum. Such men as these brought much prestige to the Academy.

Rancho La Brea and the Museum of History, Science, and Art

In 1908 an active member of the Academy, Dr. James Z. Gilbert, professor of biology at the Los Angeles High School, became interested in the Pleistocene animals found in the oil deposits at Rancho La Brea. He secured permission to begin an excavation with the help of several high school students, and gathered a collection of the fossil material for Los Angeles High School. His enthusiasm soon fired the Academy into action. Dr. Gilbert was authorized to organize a zoology section in the Academy and to begin excavation for the Academy in 1909. Finances were supplied by Dr. Hooker and the City and County of Los Angeles. Since the Academy had no building, the fossils were stored at Los Angeles High School. This interest naturally led to an association with Los Angeles County and other organizations in establishing a museum.

In the following year, the Academy entered into an agreement with Los Angeles

County, the Southern Division of the Cooper Ornithological Club, the Historical Society of Southern California, and the Fine Arts League to establish the Los Angeles Museum of History, Science, and Art. The agreement, signed on 7 February 1910, provided for a Board of Governors to be responsible for the care, supervision, control, and management of the collections. Los Angeles County would construct and maintain the building. Two members of each organization were to serve on the board. Dr. Anstruther Davidson and William A. Spalding were appointed by the Academy to fill these posts for the Academy.

On 17 December 1910 the cornerstone was laid in the presence of the Academy president, William A. Spalding, secretary Holdridge O. Collins, and George W. Parsons, along with members of the other organizations, county officials and the public. Among the documents included in the cornerstone were the Academy articles of incorporation, a history written by William H. Knight, a list of the officers and members, and volumes eight and nine of the Bulletin.

When the building was completed in late 1911, mounted skeletons from Rancho La Brea were moved from the high school into the science wing of the new museum. Other collections from the Academy were also brought to the Museum, including the library. This material was officially given to the Museum in 1931. Interest in the fossils led to the adoption of the sabertooth cat skull as the Academy emblem in 1915. In 1914 a gavel made from the wood of a McNab cypress and a vertebrae from a ground sloth, both from La Brea pits, was presented to the Academy president by Anstruther Davidson.

Meetings

Minutes of meetings during the first sixteen years have not been found, but beginning in May 1907 detailed minutes were kept, primarily because of the influence and work of Holdridge O. Collins. His meticulous records have been an invaluable source for the early history of the Academy and that of the history of the Natural History Museum.

The Academy had no home, but continued meeting on the second Tuesday evening of each month in various places until after World War II. The Chamber of Commerce Hall was mentioned most frequently, but meetings were also held in the Unity Church, Ebell Club, Women's Club, State Normal School, St. Christopher's Parlor, Friday Morning Club, Polytechnic High School, University Club, Los Angeles City Club, Union League Hall, and Burdette Hall. One had to read meeting notices carefully!

Finally in 1944 meetings were established at what was then the Museum of History, Science, and Art (now the Natural History Museum of Los Angeles County). Members gathered on the ground floor of the old building in the Division of Education lecture hall. Pot luck dinners were provided by members until 1956 when it was decided to meet for dinner in the Museum cafeteria. When the Delacour Auditorium was completed in 1960, dinner was deleted from the program and meetings were held in the auditorium. In 1924 the Academy became a part of the Pacific Division of the American Association for the Advancement of Science and in 1953 joined the national Association, took part in their meetings, and became eligible for their scholarship program.

From the beginning annual meetings had been dinner meetings held at some special place, followed by a program including a well-known speaker. But beginning in 1961, all-day meetings were organized to provide opportunities for the

presentation of papers by members. The first of these was held at Long Beach College with meetings in the following years at many state colleges, the Natural History Museum, U.S.C. and other private colleges and universities.

In November, 1969, twelve scientific societies joined with the Academy "to enrich the scientific community of Southern California," and sponsor two-day annual meetings. Several societies now offer special sessions at these meetings.

Publications

A publication program was initiated shortly after the Association was formed. Copies of these Proceedings are now out of print but a list of the first six has been recorded:

Vol. 1: July, 1886, *Catalogue of the Plants of Los Angeles County* by Anstruther Davidson
Vol. 2: August, 1896, *Eucalyptus* by Abbott Kinney
Vol. 3: April, 1897, *California Bees and their Parasites* by Anstruther Davidson
Vol. 4: 1897, *Lichens of Southern California* by Dr. Hasse
Vol. 5: July, 1897, *Seedless Plants of Southern California* by A. J. McClatchie
Vol. 6: September, 1899, *Antiseptic Vegetation for Cuba* by A. Campbell Johnston

The Bulletin of the Academy was first published in 1902 as a monthly publication. This ambitious program was more than the members could handle and after four years, issues were reduced to one, two, or three each year. Publication has continued to the present time with three Bulletins issued each year.

A monograph series, Memoirs, was begun in 1938 with *A Check List of the Macro Lepidoptera of Canada and the United States of America* by Dr. J. McDunnough. These Memoirs are either longer manuscripts, a compilation of manuscripts on a particular subject, or manuscripts from a specific symposium. The last and tenth was from the Desert Ecology Research Symposium of 1986.

No official editors have been indicated during the early years, however, Dr. Anstruther Davidson and Dr. B. R. Baumgardt, followed by Holdridge Ozro Collins, were responsible for publications for many years.

These men preserved the history of the Academy in the Bulletins. From August 1920 until his death in 1970, Dr. John Comstock was the editor. Since that time there has been a series of editors.

Sections

Monthly meetings were the pattern from the beginning until recent years. However, those with specific interests began to organize sections which met between the monthly meetings. Since the membership of these sections was usually small, members met in private homes. When attendance became too large, meetings were held in the Ebell Club or the Women's Club.

Records of the sections are sparse, but some kept records of their activities. A partial list includes: astronomical sciences, established in 1895 by J. D. Hooker, a camera group in 1896 as well as a botanical section headed by Anstruther Davidson and Theodore Payne. George Parsons and G. Major Taber formed a geological section and Dr. S. M. Woodbridge started a section on agricultural and chemical sciences. Professor B. M. Davis formed a group interested in biological

sciences in 1902 and James J. Gilbert was appointed to start a section for those interested in zoology. Some of these did not last long, others continued for many years and were still in existence until monthly meetings ceased. However, during the later years the sections did not meet but provided special programs at the monthly meetings.

There is no record of when many of the sections began to die out but they probably did not survive the depression of the thirties. At that time the Academy suffered with a low of fifty members. As the financial picture of the country returned to normal, the membership rose to 200 by 1938, gradually rising to over 400 by 1968.

A Program for Young Scientists

In 1957 a Junior Academy was introduced in the program. This was an endeavor to bring young people in to the membership. In time they were asked to participate in one program each year where several students would present papers. At other times, a student would present a paper before the regular program of the month. No separate meetings were held by the young people.

In 1980 a research program was begun by the Academy. Five high school students participated, each assigned to a research scientist for special study. The program was financed by the A.A.A.S. which provided $200.00 for each student. The following year the Arco Foundation provided money to double the program. TRW and Prentice Hall allowed the program to include twenty-four students by 1988. The Nancy Reagan Foundation added funds in 1990. At present the N.S.F. is funding the program as a part of its Young Scholars Program. The Academy, the California Museum of Science and Industry, and the University of Southern California are supporting this program. Increasing numbers of students are being added.

Students are chosen by application and recommendations from teachers. Those chosen for the program work for eight hours a week from November through mid-April. Research papers are presented at the annual meeting of the Academy. The best of these are invited to discuss their research at the national meeting of the American Junior Academy of the National Association of Academies of Sciences at the AAAS meeting.

Leadership of the Academy

Many members have contributed their time, talent, and leadership to make the Academy the strong organization it has realized over the years. It is impossible to mention all, but a list of the presidents, secretaries, and treasurers, among whom much of the work is delegated, is included.

Presidents of the Association and Academy

1891—M. H. Alter
1892—Anstruther Davidson
1894—William H. Knight
1897—William A. Spalding
1898—Abbott Kinney
1900—William H. Knight
1902—Theodore B. Comstock
1904—Melville Dozier
1906—Bernhard R. Baumgardt
1909—William A. Spalding
1913—Arthur Burnett Benton
1918—Hector Alliot
1919—Holdridge Ozro Collins
1920—F. C. Clark

1924—Mars F. Baumgardt
1925—William Alanson Bryan
1926—John Adams Comstock
1927—Samuel J. Keese
1928—George W. Parsons
1929—Ford A. Carpenter
1932—Theodore Payne
1933—Harry K. Sargent
1937—Howard R. Hill
1939—Carl Sumner Knopf
1941—R. W. Swift
1943—W. Dwight Pierce
1945—Henry James Andrews
1947—A. Weir Bell
1949—William Llewellyn Lloyd
1951—Louis C. Wheeler
1953—Sherwin Francis Wood
1955—Kenneth E. Stager
1957—Hildegarde Howard
1959—Fred S. Truxal
1961—Theodore Downs
1964—Richard B. Loomis
1966—John White
1967—Jay M. Savage
1969—William J. Morris
1971—Andrew Starrett
1973—Jules M. Crane
1975—Patrick Wells
1976—John J. Baird
1978—George Callison
1979—Takashi Hoshizaki
1981—F. G. Hochberg
1983—Richard E. Pieper
1985—Peter L. Haaker
1987—Robert G. Zahary
1988—Camm C. Swift
1991—June Lindstedt Siva

Secretaries

1891—Mary E. Hart
1893—Bernard R. Baumgardt
1906—Melvile Dozier
1908—Holdridge Ozro Collins
1912—Arthur Burnett Benton
1913—Robert Leroy Beardsley
1914—Holdridge Ozro Collins
1919—George W. Parsons
1921—John Adams Comstock
1926—R. H. Swift
1932—Howard R. Hill
1935—Carl Sumner Knopf
1939—John Adams Comstock
1948—Kenneth E. Stager
1951—Howard R. Hill
1953—Lloyd M. Martin
1954—Gretchen Sibley
1964—Charles Rozaire
1971—Patrick H. Wells
1973—Stuart L. Warter
1976—Richard E. Pieper
1981—Camm C. Swift
1988—Hans M. Bozler
1991—George Jefferson

Treasurers

1891—William Lundberg
1895—George Roughton
1896—George H. Bonebrake
1897—E. A. Praeger
1898—William H. Knight
1900—W. C. Patterson
1903—G. Major Taber
1906—Samuel J. Keese
1928—William A. Spalding
1932—Harry K. Sargent
1937—John Adams Comstock
1948—W. Dwight Pierce
1964—Russell Belous
1971—Donald R. Patten
1978—Joseph E. Haring
1981—John J. Baird
1983—Robert G. Zahary
1985—Takashi Hoshizaki
1991—Allan D. Griesemer

Acknowledgments

I would like to thank Margaret Barber, in charge of the academy office, Hildegarde Howard and Fred Truxal, former presidents and presently on the emeritus staff of the Natural History Museum of Los Angeles County for help in preparing this history. It has been difficult to find some of the information and no doubt there may be discrepancies. Some records have been lost and some are incomplete.

References Used

Historical Sketch of the Southern California Academy of Science, 1939 and 1945, authorship unknown, pamphlets.

Howard, Hildegarde. 1957. Southern California Academy of Sciences. A History Commemorating the Fiftieth Anniversary of Incorporation, 1907–1957, pamphlet.

Minutes of the Southern California Academy of Sciences, 1907–1990.

Programs of Meetings from 1905–1990.

Sibley, Gretchen. 1979. Seventieth Anniversary of Academy. Excavation at Rancho La Brea. Bull. So. Calif. Acad. Sci., 78(3):151–162.

Review Articles

This year marks the 100 year anniversary of the Southern California of Academy of Sciences. To commemorate this event, the lead article in this issue gives an historical account of the Academy written by Gretchen Sibley. Gretchen is managing editor of the Bulletin and has been associated with the Academy for 44 years.

This first issue of Volume 90 also marks the beginning of a new section of the Bulletin devoted to review articles on topics of particular interest to the southern California region. The first review is by Russell Burke et. al. and concerns the conservation of the endangered Stephen's kangaroo rat. At irregular intervals other reviews will be published. In forthcoming issues reviews on a range of topics, including monarch butterfly aggregation, and geology of seacliff retreat along the Southern California coast, will appear.

Persons interested in writing a review should send an outline of the topic, and names of referees who can comment on the appropriateness of the topic, to the technical editor. Also welcomed are suggestions for topics in need of review. Send topic suggestions and names of potential authors to me:

Jon E. Keeley, Editor
Department of Biology
Occidental College
Los Angeles, California 90041

DESERT ECOLOGY 1986
A Research Symposium

Twelve papers from the Desert Studies Consortium at the Academy 1986 Annual Meeting comprise a new publication now available. Subjects include the Coachella Valley Preserve, Water Rights, Late Pleistocene Mammals, Chemical Defense Patterns of Certain Desert Plants, Off-Road Vehicle disturbances, Desert Pupfish, Plant Communities, Desert Bats, etc.

Send name, address, and $29.00 per copy in check made out to The Southern California Academy of Sciences, 900 Exposition Blvd., Los Angeles, CA 90007.

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Conservation of the Stephens' Kangaroo Rat (*Dipodomys stephensi*): Planning for Persistence

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Abstract.—The Stephens' kangaroo rat (*Dipodomys stephensi,* Family Heteromyidae) is an endangered desert rodent of southern California. The historic range of *D. stephensi* has been severely reduced by urban and agricultural development, and remaining habitat is considerably fragmented. We estimated the minimum viable population size of *D. stephensi* from a demographic model that incorporated information about survivorship and fecundity in relation to stochastic variation in rainfall. According to the model, a population of 13,210 individuals has a 95% probability of persisting for 100 years. At a density of 10 individuals/ha, this value corresponds to a reserve size of 1321 ha. Based on this estimate and maps of current distribution, land use, and soil type, we suggested nine potential reserve sites and recommended that at least three reserves be established to secure persistence.

The Stephens' kangaroo rat [*Dipodomys stephensi* (Merriam), Family Heteromyidae] is a small nocturnal mammal currently found in three neighboring counties in southern California. Since the early 1900s, increased urbanization and agricultural development have reduced available habitat and fragmented the range of this and at least 18 other imperiled species (Table 1). Consequently, in 1988 it was listed as "endangered" by the Federal Government, and as "threatened" by the State of California Fish and Game Commission; recently California Fish and Game recommended that the species be relisted as "endangered" (Kramer 1988). In this paper, we review relevant life history and environmental information, and present a population viability analysis of *D. stephensi* with estimates of viable population sizes based on a new model of population persistence. From these results, we identify potential areas of critical habitat necessary to promote the long-term persistence of this species.

With over 500 species federally listed as endangered or threatened in the United States and its territories and possessions, the formulation of recovery plans for these species is an increasingly urgent activity. The assessment of minimum viable populations (MVP) comes from a systems approach to the vulnerability of pop-

Table 1. Threatened, endangered, and other species of concern found in areas where *D. stephensi* have been recorded. Modified from RECON (1990).

Common name	
California orcutt grass	*Orcuttia californica*
Munz's onion	*Allium fimbriatum,* var. *munzii*
Payson's jewelflower	*Caulanthus simulans*
Many-stemmed dudleya	*Dudleya multicaulis*
Palmer's grapplinghook	*Harpagonella palmer,* var. *palmer*
Thread-leaf brodiaea	*Brodiaea filifolia*
San Diego button celery	*Erynigium aristulatum,* var. *parishii*
Engelmann oak	*Quercus engelmannii*
Little mouse-tail bat	*Myosurus minimus*
San Diego horned lizard	*Phrynosoma coronatum blainvillei*
Orange-throated whiptail lizard	*Cnemidophorus hyperythrus*
Cooper's hawk	*Accipiter cooperii*
Golden eagle	*Aquila chrysaetos*
Bald eagle	*Haliaeetus leucocephalus*
Long-eared owl	*Asio otus*
California gnatcatcher	*Polioptila californica*
Coastal cactus wren	*Campylorhynchus brunneicapillus sandiegense*
Yellow-breasted chat	*Icteria virens*

ulations of a species in particular locations (Gilpin and Soulé 1986). This approach incorporates information about the demography and life history of the focal species, the environmental features critical to its survival, and relevant stochastic environmental and/or demographic events. The result, for a particular population, is an estimated minimum population size necessary for persistence over a specified time with a specified probability. Our objective for *D. stephensi* was to estimate the minimum population size that would have a 95% probability of persisting for 100 years or more.

Since species vary widely in their natural history, there is no single protocol for estimating an MVP or for determining the number of such populations. Our approach to population persistence refers not to the entire species, but to a single population. No single population should be considered representative of the species as a whole. Therefore it would be unconscionable to base the persistence of an entire species upon a single population (Soulé 1987a), unless only one population remains with no possibility of reintroduction. Hence, our results should not be construed to indicate that a single population of any particular size is sufficient or appropriate for the conservation of this species.

For *D. stephensi,* only limited information is available about demography, current population sizes, and environmental factors affecting distribution and abundance. However, such information is available for closely related species, such as *D. agilis,* which occupies much of the range of *D. stephensi.* In modeling population persistence, we utilized information about the natural history of *D. stephensi* and other related species from both published literature and unpublished surveys. In addition, we compiled information about historical rainfall patterns in the current range of *D. stephensi.* Model results indicate that the MVP size that will persist for at least 100 years with a probability of 95% is 13,210 individuals. This value probably exceeds the total population of *D. stephensi* outside the

Warner Ranch population, suggesting that the current fragmented populations are in urgent need of intensive management. Given these results and the distribution of suitable soils in relation to current populations of *D. stephensi,* we suggest a minimum of three areas as critical habitat for the recovery and persistence of this species throughout its current geographic range.

Below, we first review the natural history of *D. stephensi,* environmental variables related to its abundance, and the population dynamics of the demographic model. Then we present model results for a range of persistence times and probabilities. The estimates of MVP size, along with maps of current distribution, land use, and potential habitat, form the basis for identification of critical habitat areas, suboptimal habitats that can be upgraded, and potential corridors between current populations. Additional management activities to promote the persistence of *D. stephensi* are also suggested.

Natural History of *Dipodomys stephensi*

Description and Taxonomy

Dipodomys stephensi is a medium-sized member of the rodent family Heteromyidae. North American heteromyids are an ecologically uniform group of nocturnal, burrowing granivores of arid regions. *D. stephensi* is similar to other kangaroo rats in having external cheek pouches, large hind legs and relatively small front legs. The average adult weight is 67 g and total adult body plus tail lengths range between 227 and 300 mm (Bleich 1977). The tail is crested and bicolored, and is 1.45 times the length of head and body. *D. stephensi* is morphologically similar to *D. agilis,* a sympatric species, but differs in external and cranial characteristics (Bleich 1977).

The relationship of *D. stephensi* to other species of *Dipodomys* is reviewed by Bleich (1977). Best and Schnell (1974) included *D. stephensi* in a phenetic cluster with *D. ordii, D. gravipes, D. heermanni, D. ingens, D. ornatus,* and *D. elator,* based on similarity of bacula. However, this grouping is not stable when other characteristics are considered (Schnell et al. 1978), and no cladistic analysis is available for species of *Dipodomys.* Using karyological evidence, Stock (1974) concluded that *D. stephensi* is closely related to *D. gravipes.* Though sympatric with *D. agilis* and similar in morphology, *D. stephensi* probably does not hybridize with *D. agilis* due to a difference in fundamental chromosome number (Lackey 1967a). Friesen (1986) proposed that morphological similarities between *D. stephensi* and *D. agilis* result from similar environmental pressures, rather than close genetic relatedness.

Distribution and Abundance

The distribution of *D. stephensi* covers parts of three neighboring counties in the San Jacinto Valley of southern California (Fig. 1). Most of the range occurs in western Riverside County, with the northern end of the present range extending into southwestern San Bernardino County and the southern portion into northern San Diego County. Accurate mapping of *D. stephensi* distribution is difficult because individuals spend little time above ground (approximately one hour per night, O'Farrell pers. comm. 1989), and trapping success is inconsistent. However, two major attempts to map the distribution of *D. stephensi* were recently completed (Price and Endo 1989; O'Farrell and Uptain 1989).

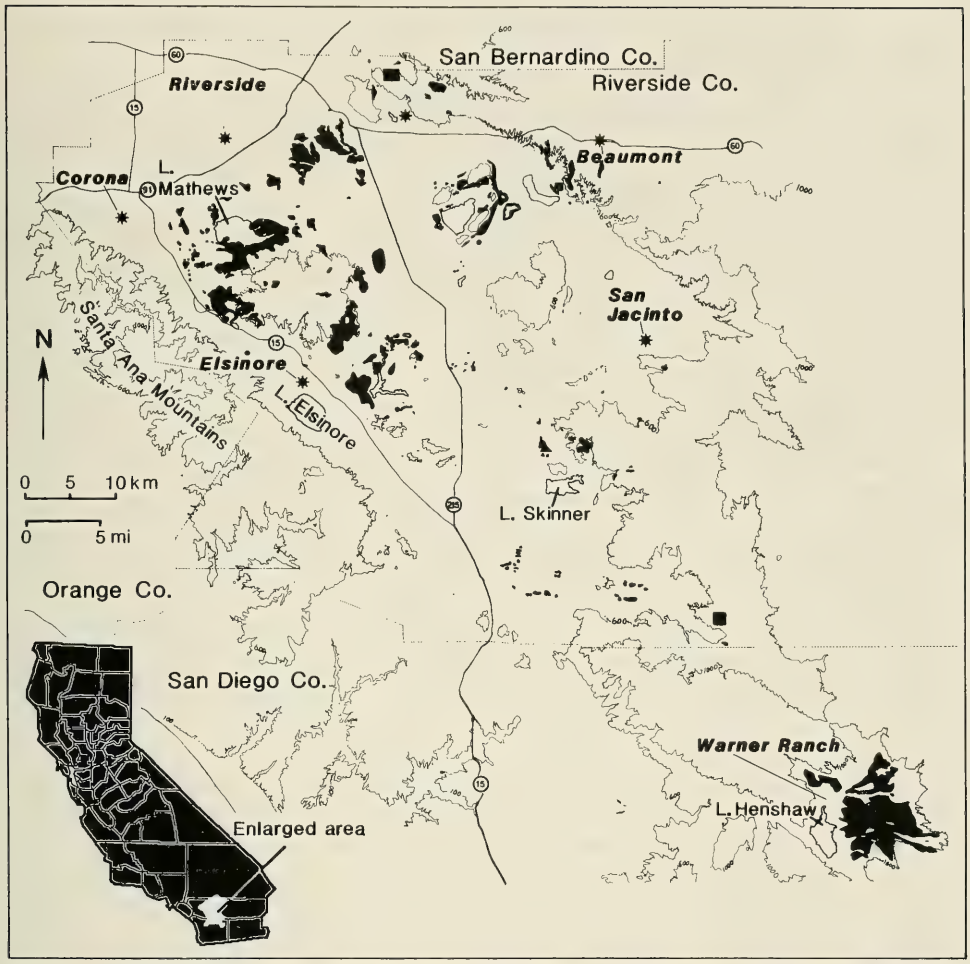

Fig. 1. Distribution of *D. stephensi* in San Bernardino, Riverside, and San Diego counties, California. Darkened areas are sites surveyed by O'Farrell and Uptain (1989) with either known presence or suitable habitat without confirmed presence. Also indicated are highways and topographic contours (100 m, 600 m, 1000 m).

Price and Endo (1989) estimated the historical distribution of *D. stephensi* (before 1938 and in 1938) and the present distribution (in 1984) in Riverside County, California. The distributions of soil types that currently support *D. stephensi* were used to reconstruct the historical distribution of sparse annual grasslands following settlement by Spanish ranchers. Under the assumption that the current association between occupied habitat and soil type reflects original distribution, the historic range of *D. stephensi* was inferred from the original distribution of grassland. Before 1938, 124,774 ha of western Riverside County supported suitable habitat. By 1938, only 45,569 ha (37%) of suitable habitat remained undeveloped. Fragmentation of habitat occurred along with habitat reduction. By 1938, 83% of the patches of potential habitat were smaller than one km^2 (100 ha) and mean patch size was 77 ha. In 1984, only 8588 ha remained in patches greater

than one km^2. Sixty percent of pre-1938 habitat was lost, suggesting that the population has also decreased by 60% (Price and Endo 1989).

O'Farrell and Uptain (1989) published detailed maps along with the results of an extensive survey using burrows, runways, scats, and other surface indicators seen along strip transects of dirt roads and trails. They documented 79 extant populations of *D. stephensi* occurring primarily in habitat patches of 8 to 420 ha, with 64% of these populations inhabiting patches of 8 to 42 ha. Most of these populations occur in western Riverside County. However, the largest population of *D. stephensi,* estimated at 14,000 individuals, resides on the Warner Ranch near Lake Henshaw, San Diego County (O'Farrell and Uptain 1987), although this population is probably declining (O'Farrell and Uptain 1989). Occupied habitats are found from approximately 35 m to about 1100 m in elevation (O'Farrell and Uptain 1989). While most extant populations occur below 600 m, Warner Ranch is at the highest elevation (830 to 1100 m).

The San Jacinto Valley, except for the remote areas west and south of Lake Mathews, is undergoing rapid urbanization (Fig. 2). *D. stephensi* is much less abundant in the central and eastern portions of the valley where agricultural conversion has been concentrated. Urban development extends from Sunnymead in the north to Sun City and Elsinore in the south, further restricting the remaining populations in the center of the valley. Numerous, small populations have been virtually eliminated along the fringes of the historical range in San Bernardino and San Diego Counties, east toward the Badlands, and south of Beaumont in Riverside County (O'Farrell and Uptain 1989).

Trapping response varies considerably among seasons and among years depending on the productivity of vegetation (O'Farrell and Uptain 1987). Density varies by more than an order of magnitude within populations of *D. stephensi* (Price and Endo 1989). The highest reported density is >50 individuals per ha during the summer months (Thomas 1975). Fall and winter densities range from 6 to 15 individuals per ha (Hogan 1981). According to O'Farrell and Uptain (1989), most of the currently occupied habitats contain populations of low (5 individuals per ha) or medium density (5 to 10 per ha), and only a few areas contain a high population density (≥ 10 per ha). Bleich (1977) reported summer population densities of 7.5 per ha in the annual grassland community, and a density of 33.8 per ha in the *Haplopappus* association of the coastal sage scrub community. Acquisition of information about movements of individuals may require revision of these estimates.

Habitat Requirements

Dipodomys stephensi is found primarily in coastal sage scrub or annual grassland habitat where perennial cover is less than 30% (Lackey 1967a, Bleich and Schwartz 1974, Hogan 1981, O'Farrell and Clark 1987). Lackey (1967a) and Bleich (1977) also reported *D. stephensi* in more open habitat. Forb seeds are the preferred food; densities are highest where the proportion of annual forbs to grasses is near one (O'Farrell and Clark 1987; O'Farrell and Uptain 1987, 1989). Unlike grasses, forbs tend to disarticulate rapidly after drying, resulting in bare patches of ground.

Vegetation most commonly associated with *D. stephensi* includes the shrubs *Artemesia californica* and *Eriogonum fasciculatum,* and the herb filaree, *Erodium cicutarium* (O'Farrell and Clark 1987, Kramer 1988). O'Farrell and Uptain (1989)

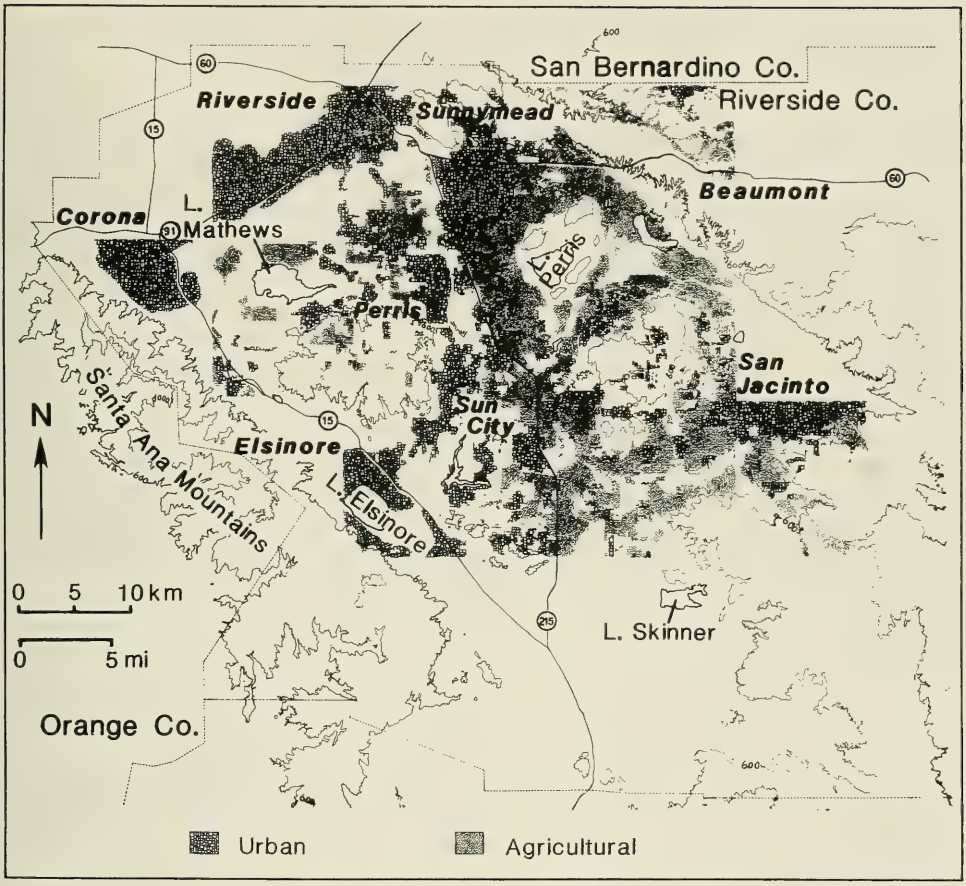

Fig. 2. Land-use patterns in western Riverside County (urban and agricultural) from the 1984 Upper Santa Ana River Drainage Area Land Use Survey.

found that populations of *D. stephensi* decreased as bunchgrass (*Aristida* spp.) density increased. Their survey indicated that *D. stephensi* occurs primarily in intermediate seral stages of vegetation.

Soil type also influences distribution, and has been shown to be a significant predictor of the presence or absence of *D. stephensi* (Price and Endo 1989). O'Farrell and Uptain (1989) found extant populations on 36 types of well-drained soils. In the Santa Ana Mountains, both Pequegnat (1951) and Bleich (1977) found *D. stephensi* on gravelly soils. Patches of fine-grained soil may be needed for sandbathing; Eisenberg (1963) reported that the pelage of *Dipodomys* becomes matted and greasy if no sand is present for sandbathing. *D. stephensi* generally does not occur on clay soils, presumably because of the difficulty of burrowing in clay. Since burrows are often as deep as 45 cm or more, soil cover of occupied habitat is generally at least 0.5 m deep (Price and Endo 1989). O'Farrell and Clark (1987) found that *D. stephensi* prefers habitats low in rock cover.

D. stephensi inhabits land forms that are relatively level or gently sloping. O'Farrell and Uptain (1989) found *D. stephensi* occupying slopes of 0 to 50%.

Moore-Craig (1984) indicated that *D. stephensi* preferred areas with a slope of 7 to 10%.

Behavior

Dipodomys stephensi is a nocturnal, solitary mammal and little is known of its social behavior. Intraspecific aggression has been reported in most species of *Dipodomys* (Eisenberg 1963). In *D. merriami,* females have non-overlapping home ranges; conversely, males have overlapping ranges with both males and females, but exclusive centers of activity (Reynolds 1958).

Dispersal distances are unknown for *D. stephensi.* However, Jones (1989) reports lifetime dispersal distances for *D. merriami* of 0 to 265 m for males and 0 to 158 m for females. Using radiotelemetry, he determined that most nightly movements were in radii of familiarity and that dispersal consisted of a series of small shifts in centers of activity within familiar areas.

Mating behavior is known only for other species in this genus. *Dipodomys* males of two species go to the home areas of neighboring estrus females to mate (Randall 1987). If more than one male is present, they may compete for access to females by chasing each other or engaging in foot-drumming. Randall (1987) observed females mating with more than one male in *D. merriami* and *D. spectabilis.*

Reproductive Biology

Based on trapping data for pregnant females and males with scrotal testes, Lackey (1967b) and Bleich (1973) concluded that the mating season for *D. stephensi* is late spring and early summer. O'Farrell and Clark (1987), however, found scrotal males and females in estrus, pregnant, and/or lactating in July, suggesting either an extended breeding season or another late summer reproductive season. The mean litter size for *D. stephensi* in the wild is unknown, but for females brought into a laboratory, Lackey (1967b) reported an average litter size of 2.67 offspring (16 offspring in six different litters).

Age at maturity is not known for *D. stephensi,* but in some years, young-of-the-year may reproduce (Price pers. comm. 1989). Under high rainfall conditions, females may produce two litters in one spring/summer season, and females born early in the season may mature quickly and produce their first litters by the end of the summer; with little rainfall, reproduction may be suspended and survivorship can be low (O'Farrell pers. comm. 1989; Price pers. comm. 1989).

Nesting behavior has not been studied in the field. Lackey (1967b) reported that females in captivity began construction of elaborate nests up to one week before parturition. Thomas (1975, cited in Bleich 1977) speculated that *D. stephensi* uses old pocket gopher (*Thomomys bottae*) burrows; burrows of the California ground squirrel (*Spermophilus beecheyi*) may also be used (O'Farrell and Uptain 1989).

Interactions With Other Species

Predators of *D. stephensi* are probably similar to those of other desert rodents, and include owls, snakes, foxes, coyotes, and feral cats (Munger et al. 1983). Owl pellet analysis revealed that *D. stephensi* comprises a portion of the diet of barn owls (*Tyto alba*) and long-eared owls (*Asio otus*) (Bleich 1977). Reichman (1983) and Price and Brown (1983) suggested that predator avoidance may be important

in determining microhabitat use for foraging and home range of desert rodents. Compared to *D. agilis, D. stephensi* is significantly more likely to forage in open, lit spaces, possibly leading to greater owl predation (Price and Longland, in review).

Information on interspecific competition in the genus *Dipodomys* is primarily limited to other species of *Dipodomys. D. agilis* is the only congener broadly sympatric with *D. stephensi*; it is similar in both size and ecology (Price and Endo 1989). However, Munger et al. (1983) and Schroder (1987) postulated that competition among *Dipodomys* species may be uncommon. Price and Longland (in review) suggest that interactions of factors relating to water balance, foraging economics, and predation risk may result in divergent habitat associations between *D. stephensi* and *D. agilis.* Although in captivity, *D. agilis* attacked *D. stephensi* and won aggressive encounters (Stock 1974), habitat specialization may greatly limit interaction between the two species in the wild (O'Farrell pers. comm. 1989).

Little is known of disease or parasitism in species of *Dipodomys.* Hill and Best (1985) examined the levels of coccidia infection in five species of southern California *Dipodomys* (not including *D. stephensi*) and found that infection levels were generally low (8%). However, Stout and Duszynski (1983) found oocysts of coccidia in the feces of 32 of 71 (45%) individuals of *D. agilis* and 43 of 124 (35%) individuals of *D. merriami.* The importance of these and other parasites on desert rodent populations has not been assessed (Munger et al. 1983).

Reasons for Decline

The major reason for decline in *D. stephensi* has been a reduction in habitat (Fig. 2). Currently, *D. stephensi* occupies an unusually small range for rodents in general, and for kangaroo rats in particular (Price and Endo 1989). After 1984, habitat loss accelerated as urban development outpaced agricultural development (Kramer 1988). Agricultural development may be a less serious long-term threat, because *D. stephensi* can recolonize abandoned agricultural land (Thomas 1975).

Decline of available habitat is expected to continue because existing state regulations and county zoning restrictions do not provide adequate protection for *D. stephensi* habitats. Riverside County's General Plan guidelines have zoned 79% of the occupied sites for uses incompatible with the preservation of *D. stephensi* (Kramer 1988). Three percent of the county was zoned for protection of wildlife or vegetation, but many of these areas are not specifically suitable for *D. stephensi.* Only 6% of the range of *D. stephensi* has been zoned for uses compatible with its preservation (Kramer 1988). In 1989, the governments of Riverside county and the cities of Riverside, Moreno Valley, Lake Elsinore, Hemet, and Perris applied to the U.S. Fish and Wildlife Service for a Section 10(a) permit (under the federal Endangered Species Act of 1973) to "take" *D. stephensi* in the process of development projects. At the same time, they submitted a short-term interim Habitat Conservation Plan. Approval of the permit would allow the destruction of 4400 acres (1760 ha) of the remaining occupied habitat in exchange for the purchase of an equivalent amount of land (not necessarily occupied) to be managed for long-term survival of the species (E.I.S. 1990). The U.S. Fish and Wildlife Service and the applicants released a joint Environmental Impact Statement and Environmental Impact Report (E.I.S.) in March 1990. This extensive document includes consideration of several alternatives for conservation of the species and

their potential economic impacts, the establishment and placement of "study areas" (=preserves), and the need for more extensive study of the species itself.

Reduction in habitat (Fig. 2) has also resulted in greater habitat fragmentation (Price and Endo 1989). For example, on the east side of San Jacinto valley, *D. stephensi* is restricted mainly to the edges of plowed fields (Kramer 1988). Fragmented, small populations are more vulnerable to environmental and demographic stochasticity such as drought, fluctuations in birth or death rates, unequal sex ratios, and a loss of genetic diversity (Soulé and Wilcox 1980).

Other factors may also be important in reduction of *D. stephensi* populations. Populations near urban areas may be vulnerable to predation by domestic or feral cats, and other predators associated with humans (e.g., Soulé et al. 1988). *D. stephensi* may also be vulnerable to off-road vehicle activity and to rodent control programs on both state recreation areas and farms. In addition, some landowners or project developers, presumably to avoid federal or state restrictions of their land use activities, have disked or plowed their land after detecting the presence of *D. stephensi* (Kramer 1988).

Environmental Variables Affecting Abundance

Rainfall, vegetation, and elevation are correlated with distribution and abundance of *D. stephensi*. In this section, we demonstrate how these variables can be used as predictors of *D. stephensi* abundance. First, rainfall and rodent abundance are correlated. Then, variation in rainfall over the geographic range of *D. stephensi* is analyzed to quantify environmental heterogeneity. Finally, we analyze the effect of vegetation type and elevation on *D. stephensi* abundance.

Statistical Methods

We compared monthly rainfall to the census counts of two other heteromyid rodents, *D. agilis* and *Chaetodipus fallax* (*Perognathus fallax*), using forward stepwise regression with alpha-add = 0.10 and alpha-delete = 0.15 (Neter et al. 1985). Riverside County monthly rainfall records, during the rainy season (October through May) for the years 1979 to 1987 were used as the independent variables; the dependent variable was abundance as measured by annual trapping data in the fall, for the years 1980 to 1988 (Price and Endo 1989).

We also evaluated the covariation of precipitation at three weather stations within the *D. stephensi* range—Beaumont (33°56′ lat., 116°58′W long., 792 m), Riverside (33°57′ lat., 117°23′W long., 256 m), and Elsinore (33°40′ lat., 117°20′W long., 391 m)—using 70 years of annual rainfall data (NOAA 1917–1987). The relationship between each pair of rain stations was calculated using simple linear regression at the 0.05 level of significance (Neter et al. 1985). Since the total annual rainfall data from the three locations were not normally distributed, the data were normalized by transformation to natural logarithms. A one-way ANOVA, with a 0.05 level of significance, was performed to test for equality among the three sites (Neter et al. 1985).

Abundance measures of *D. stephensi* in relation to vegetation type and elevation at 66 sites were taken from O'Farrell and Uptain (1989). Estimating the effects of vegetation and elevation effects required modification of their data. O'Farrell and Uptain assigned four categories of relative abundance ("trace," "low," "medium," and "high") based on surface indicators of *Dipodomys* activity including

burrows, runways, and scat. Some sites contained only one level of abundance, while others contained both trace and low abundance levels or both low and medium abundance levels. We therefore ranked relative abundance of *D. stephensi* for each site as one of five levels: 1 = trace, 2 = trace/low, 3 = low, 4 = low/medium, 5 = medium. Level 2 (trace/low) and Level 4 (low/medium) were created for sites that contained at least 25% of one of the two abundance categories. O'Farrell and Uptain found areas of high abundance only nested within sites containing primarily medium abundance; thus Level 5 includes sites that contain some amount of high abundance.

For the statistical procedure, sites were classified as either low elevation ($\leq$610 m) or high elevation (>610 m), and as either "grassland only" or "grassland only" or "grassland with scrub," based on notes by O'Farrell and Uptain (1989). The modified data set was tested with an unbalanced two-way ANOVA for vegetation and elevation, fixed effects, with a 0.05 level of significance (Neter et al. 1985).

Correlation of Rodent Abundance and Rainfall

Price and Endo (1989) observed that fall rodent populations in Riverside County fluctuated widely over time by at least two orders of magnitude, and were correlated with annual rainfall. The results of our stepwise regression of population density against monthly rainfall indicate that March rainfall is the best predictor of fall desert rodent abundance. There is a significant positive linear relationship (Figs. 3a, b) for both *D. agilis* ($N = 8$, $R^2adj = 0.776$, $P = 0.002$) and *Chaetodipus fallax* (*Perognathus fallax*) ($N = 8$, $R^2adj = 0.930$, $P \leq 0.0005$) between fall abundance and rainfall in March preceding the census.

Because *D. agilis* and *C. fallax* are in the same family as *D. stephensi* and are also desert-living granivores, we infer that *D. stephensi* abundance is also likely to fluctuate in accordance with March rainfall. This inference has important implications for management of the species. If March rains are lower than average, indicating stress or drought, then efforts to improve fall *D. stephensi* recruitment can begin the spring of the preceding year. Monitoring March rainfall may allow managers not only to predict populations in the coming fall and winter, but also to decide if interventions to enhance recruitment (such as food provisioning) are necessary.

Regional Rainfall Covariation

Annual variation in rainfall is highly correlated between all three pairs of rain stations. The results of the simple linear regressions between pairs of stations (Fig. 4) show significant, positive, linear relationships between all pairs (Beaumont vs. Elsinore, $N = 65$, $r^2 = 0.859$, $P < 0.0005$; Beaumont vs. Riverside, $N = 70$, $r^2 = 0.864$, $P < 0.0005$; Riverside vs. Elsinore, $N = 65$, $r^2 = 0.858$, $P < 0.0005$). This pattern implies that temporal patterns of rainfall variation throughout this area are homogeneous, and consequently that population fluctuations and viability of *D. stephensi* will be highly correlated throughout much of the species' range.

Price and Endo (1989) recommended that the best way to guard against environmental catastrophe such as drought is to designate a few large reserves, placed as far apart as possible, so that if *D. stephensi* is extirpated from one reserve, other populations will likely persist and can serve as restocking sources. However, if the *D. stephensi* range is a homogeneous climatic region as our analysis suggests,

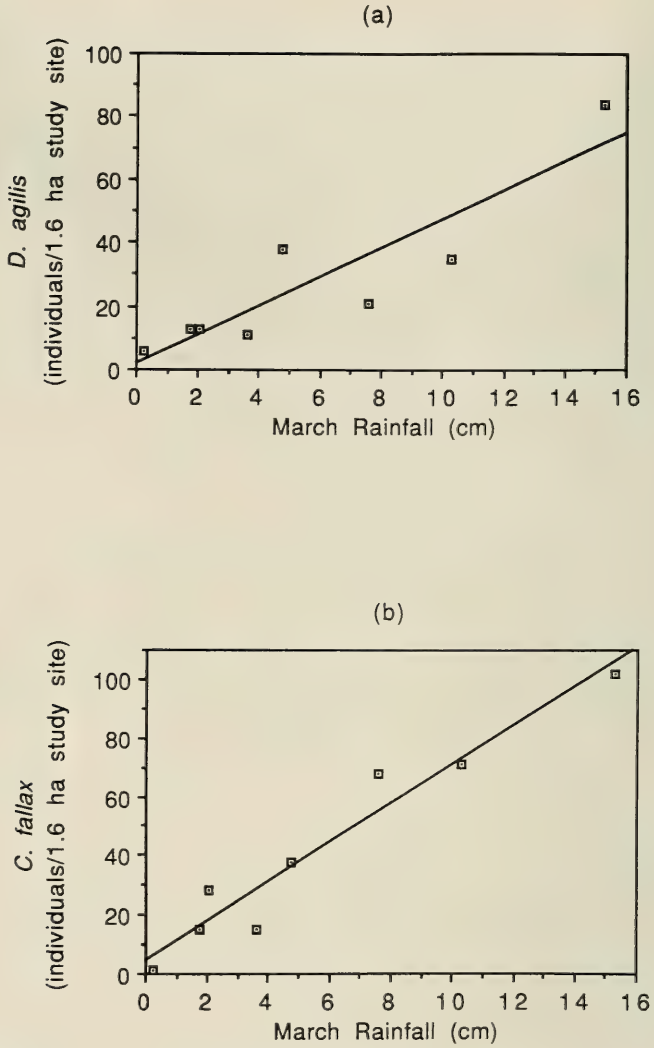

Fig. 3. Relationship between March rainfall and fall abundance for *D. agilis* (a) and *P. fallax* (b). Rodent data, from Price and Endo (1989), represent total number of individuals on 1.6 ha study site. Rainfall data from Riverside weather station.

then distance between reserves within the current range cannot guard against the impacts of drought. A better way to buffer the species against a series of very dry years may be to rely on the fortuitous survival of *D. stephensi* in refuges with higher than average rainfall. The locations of such potential refuges should be an object of future study. In addition, corridors of appropriate habitat between reserves could allow for recolonization from populated areas to extirpated patches.

Regional Rainfall Amounts

Although rainfall is highly correlated among rain stations, results of the one-way ANOVA of differences in log annual rainfall among rain stations show a

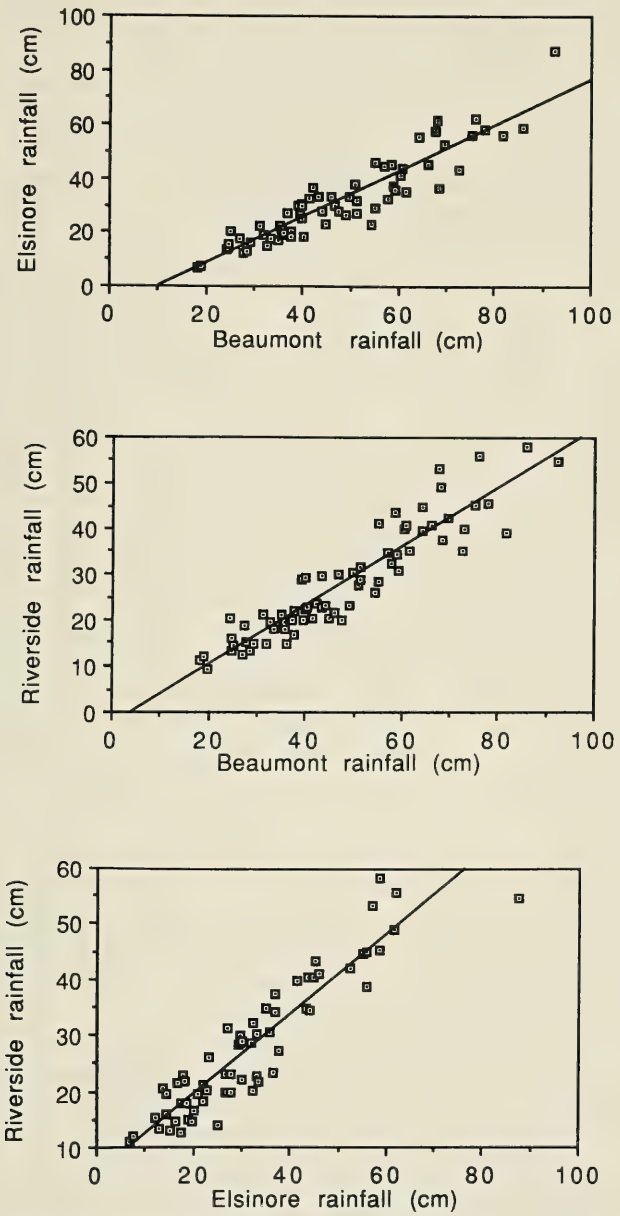

Fig. 4. Pairwise scatterplots of annual rainfall (cm) at three weather stations, Beaumont, Riverside, and Elsinore, with *D. stephensi* range.

significant difference among the means at Beaumont, Riverside, and Elsinore (Table 2). Beaumont, a station of much higher elevation than the other two stations, receives significantly more annual rain than either Riverside or Elsinore (Fig. 5). These results have important implications for *D. stephensi* management. If higher elevations receive more rain than lower elevations, then in periods of severe drought, high elevations may serve as refuges. If, in placing reserves as far

Table 2. Results of one-way ANOVA to test for differences among mean rainfall at three rain stations (N = 208), as shown in Figure 5.

Source of variation	Sum of Squares	df	Mean Square	F-ratio	*P*
Site	12.7	2	6.4	31.8	<0.05
Error	41.0	205	0.2		

apart as possible, as suggested by Price and Endo (1989), some reserves are located near Beaumont and Warner's ranch (see Fig. 1), then their suggestion is consistent with our later recommendations.

Effect of Vegetation and Elevation on Abundance

Results of the two-way ANOVA of vegetation and elevation effects on *D. stephensi* abundance (Table 3) indicate a significant difference between the means related to vegetation type but not to elevation, nor is there any significant interaction effect. *D. stephensi* is significantly more abundant in "grassland only" vegetation than in "grassland with shrub" vegetation, regardless of the elevation (Fig. 6). These results should be interpreted with caution, however, because a large portion of the variability is unexplained; the sum of squares of the error (SSE) is quite large. This large component of random variation around the means of the factor levels may indicate the omission of one or more important independent variables. It is likely that inclusion of additional independent variables, such as soil type, slope, and presence of competitors, would help to reduce this error.

Population Dynamics Analysis

We used a stochastic model of population persistence to estimate the size of a minimum viable population (MVP) (Shaffer 1981) of *D. stephensi.* The model is specifically designed to simulate the population dynamics of species with "boom-or-bust" type life histories, such as *D. stephensi.* For this analysis we consider a "population" to be a commonly interbreeding collection of individuals that are free to disperse within a limited geographical area. Therefore, results should not be misinterpreted to suggest that a *single* population of any particular size is sufficient or appropriate for conservation of the entire species.

Rather than a single MVP size, the model can generate an infinite number of such estimates depending on demographic assumptions, choice of persistence time, and level of confidence desired. Predictions of population persistence must necessarily be qualified with two conditions—the accepted failure rate and population persistence time (Soulé 1987a). The failure rate is the percentage of simulations in which the population goes extinct before the end of the simulation. Population persistence time is the length of time or number of generations the simulation is to model.

The BOOMBUST model used for these predictions is described in detail elsewhere (Burke and Burke, in prep.). Other, more commonly available models were considered, but were rejected because they required life history information that was not available for this species, included interactions that were not important to this species, and/or lacked a mechanism to relate environmental variation to

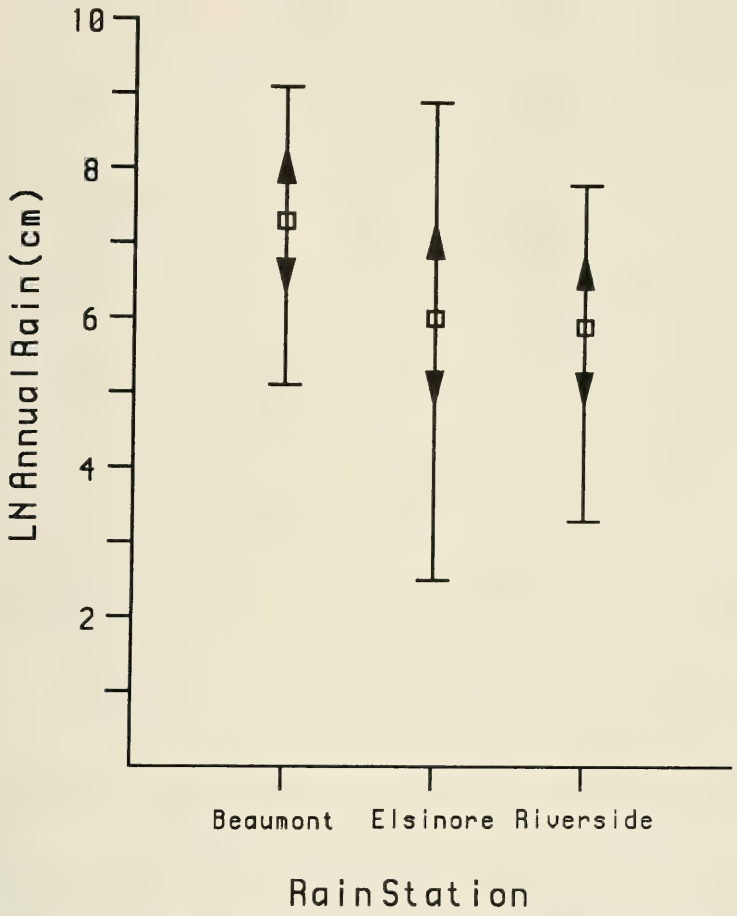

Fig. 5. Comparison of total rainfall among three rain stations within *D. stephensi* range. Open box is mean, vertical line is range, arrow is one standard deviation from the mean.

demographic parameters. BOOMBUST simulates the population dynamics of species whose fecundity and survivorship covary and are correlated with a single dominant environmental variable such as rainfall. This relationship, common for desert rodents (Munger et al. 1983), tends to result in "boom or bust" life histories. For example, Price and Endo (1989) found a high correlation between rainfall and population fluctuations of two sympatric rodent species. The impact of rainfall is introduced into the BOOMBUST simulation through the use of annual rainfall

Table 3. Results of two-way ANOVA to test for effects of habitat (grassland-only vs. grassland-with-shrub) and elevation (high vs. low), (N = 208), as shown in Figure 6.

Source of variation	Sum of Squares	df	Mean Square	F-ratio	*P*
Habitat	7.313	1	7.313	4.870	0.031
Elevation	0.563	1	0.563	0.375	0.543
Interaction	2.864	1	2.864	1.907	0.172
Error	93.107	62	1.50		

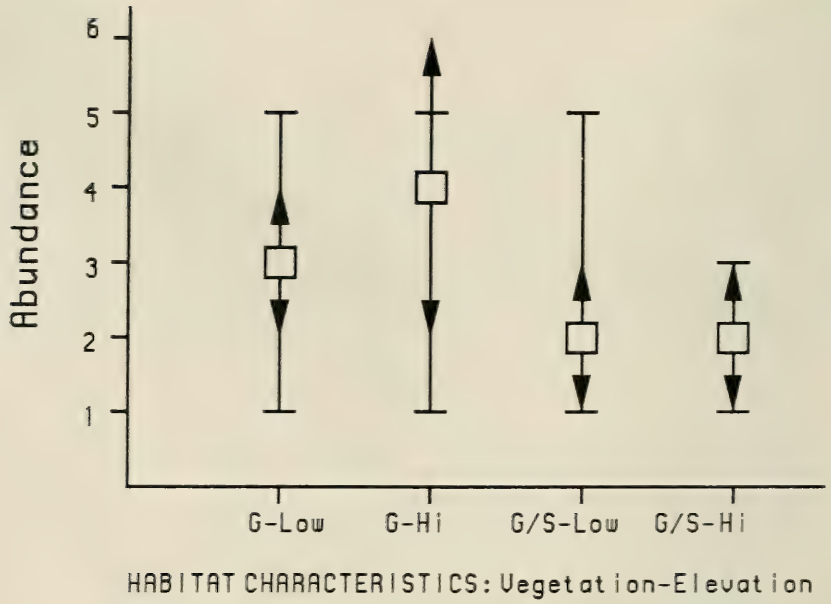

Fig. 6. Abundance of *D. stephensi* in relation to vegetation and elevation. G-Low is grassland at low elevation; G-Hi is grassland at high elevation; G/S-Low is grassland and shrub at low elevation; G/S-Hi is grassland and shrub at high elevation. Open box is mean, vertical line is range, arrow is one standard deviation around the mean.

records from within the geographic range of *D. stephensi,* in order to set both survivorship and fecundity rates in each iteration.

The BOOMBUST model therefore accounts only for environmental stochasticity, one of the two general classes of random demographic factors (Shaffer 1987; Lande 1988). Demographic stochasticity, which includes random fluctuations in age structure, sex ratio, inbreeding, and other factors, varies in importance inversely with population size and is far more difficult to estimate and model meaningfully. Its exclusion from our analysis probably means that our MVP size estimates are minimal.

Another factor not considered by the model is effective population size (Lande and Barrowclough 1987), which can be a concern when appropriate levels of genetic variation are at risk. However, loss of genetic variation is probably a relatively minor problem for species such as *Dipodomys stephensi,* which appear to be characterized by recovery from population crashes in a few generations. When periods of low population levels are brief, it is unlikely that much genetic variation will be lost (Lande and Barrowclough 1987). Populations simulated by BOOMBUST rarely stayed low for long, rather they went extinct or rapidly climbed to high levels. However, because maintenance of genetic variation was not considered in the model, it is important to point out how populations simulated by the BOOMBUST model compare to one in which census size equals effective population size. We assumed that at a given level of rainfall, all individuals within each of the two age classes have the same probability of survivorship and reproduction, i.e., that all individuals within an age class are equivalent. This does not mean that all females necessarily breed in each simulation year, only that each

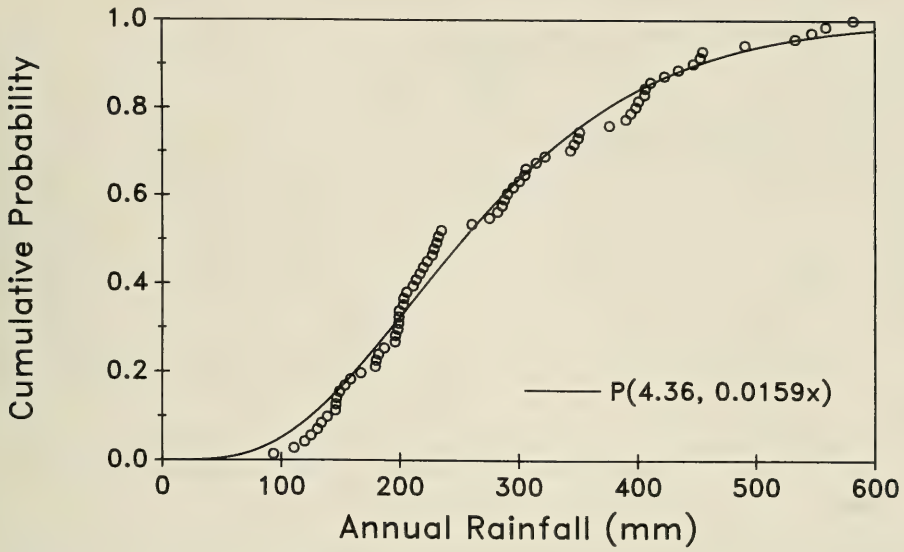

Fig. 7. Cumulative rainfall plot with incomplete gamma function fit. Points are rainfall data from Riverside, California, 1914–1987; solid line is fitted function. Parameter a, bx indicated.

has an equivalent likelihood of breeding. Although we modeled only females, in calculating total population sizes, we added an equal number of males, assuming a 1:1 breeding sex ratio. To the extent that females within an age class are not equivalent and that male reproductive success varies, the MVP estimates are minimal.

Using the Marquardt algorithm for nonlinear least squares fit, the cumulative probability of annual rainfall from the NOAA station at Riverside, CA, from 1914 to 1987 was fit to an incomplete gamma function (Fig. 7), which is equivalent to a cumulative Poisson distribution of the general form P(a, bx) (Sokal and Rohlf 1981). The fitted median rainfall ($P = 0.50$) is 253.8 mm per year. From the fitted function, 100 artificial, 200-yr rainfall records were randomly generated and used as stochastic input into BOOMBUST.

Based on available life history information discussed earlier, we estimated the relationship between rainfall and the relevant survivorship and fecundity parameters (Fig. 8). These relationships were used as assumptions and inputs in the BOOMBUST model, which simulates the survivorship and fecundity of female members of the population. The maximum age of an individual was limited to four years. Fecundity of females one year of age or older was set at 1.7 female offspring per litter, while females which bred in their first summer were assumed to produce litters of 1.5 female young per litter. To model the occasional second breeding of adult females in a single year, as well as occasional reproduction by young-of-the-year, the following relationship was used:

$$\text{Summer brood} = \text{fecundity of 1st brood} \cdot 1 - e^{c(\text{rainfall-rainfall/median})}$$

The coefficient c was set so that when rainfall equaled twice the median value, 75% of the adult females would have a second brood, and 75% of the young-of-the-year would have a litter in their first year.

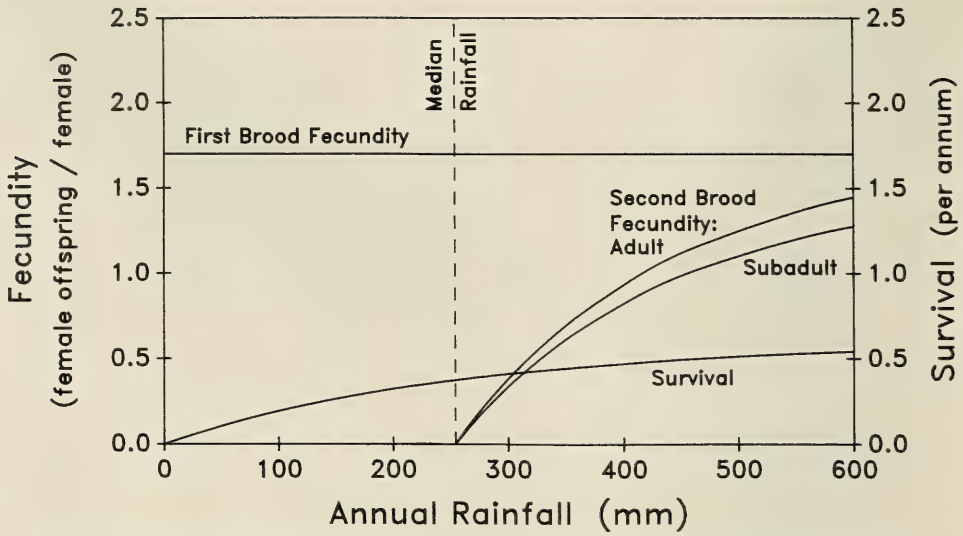

Fig. 8. Relationships between life history traits and rainfall assumed for BOOMBUST model.

To calculate survivorship as a function of rainfall, we assumed that: 1) at zero rainfall (which has never occurred since rainfall has been recorded), the population would go extinct in one year; 2) under the most favorable rainfall conditions, annual survivorship would asymptotically approach 0.6 (Zeng and Brown 1987); and 3) if annual rainfall were constant at the median value, the intrinsic population growth rate would be unity. These assumptions can be conveniently integrated into a survivorship function of the form:

$$\text{Survivorship} = a(1 - e^{-b \cdot x \cdot \text{rainfall}}),$$

where *a* equals 0.6, and *b*, to satisfy assumption 3) and the stated fecundity, equals 0.0982. Using this formula, in years of median rainfall, annual survivorship is 0.375, which compares well with the results of Zeng and Brown (1987). Finally, the total population was additionally constrained not to exceed a hundredfold increase over the initial population size, thereby establishing a finite carrying capacity of the environment under the most favorable conditions.

Various initial population sizes, ranging from 32 up to 1,000,000 females, were analyzed for probability of persistence, using the generated artificial rainfall records. Figure 9 illustrates the relationship between probability of population persistence and initial population size for three different time spans: 50, 100, and 200 years. The probability of extinction of a population was strongly dependent on the size of the initial population. Five hundred simulation runs were used to generate a mean probability and standard deviation for each time span.

A manager interested in maintaining a population with a 0.95 probability of persistence for 200 years would find that $10^{4.09}$ (=12,302) females are required in the initial population. The large initial population sizes required for long term persistence are indicative of the numerous constrictions in population size (bottlenecks) resulting from random occurrences of unfavorable years of low rainfall. As expected, the probability of population persistence of any given initial size

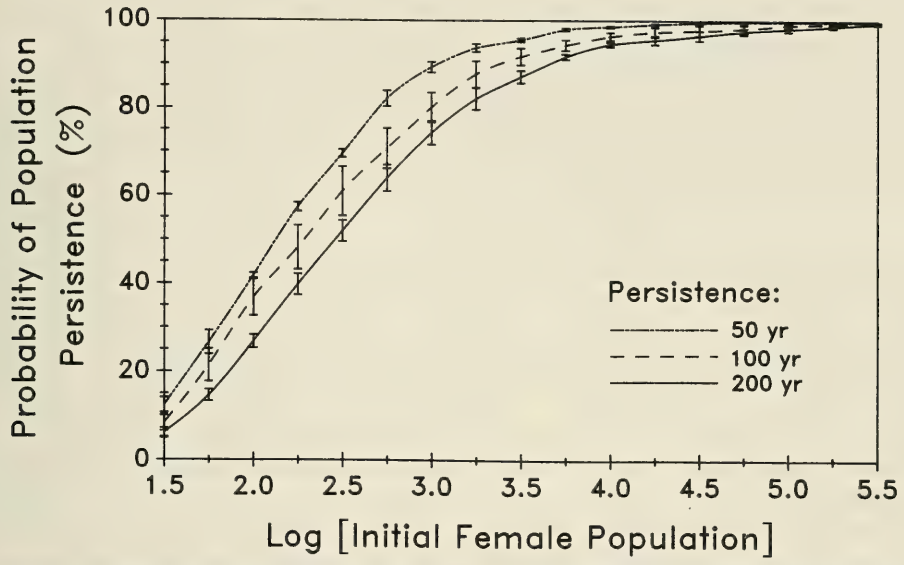

Fig. 9. Probability of population persistence for 50, 100, and 200 years as a function of natural log of initial female population size. Error bars are one standard deviation around the mean.

decreases as greater lengths of time are considered. However, all three curves level off when initial female population sizes are greater than $10^{3.75}$, indicating that beyond this point, further increases in initial population size do not substantially improve persistence probabilities over each time period.

Table 4 summarizes the results of Figure 9 at some convenient points, and presents the results for selected combinations of persistence probability and modeled time span. Because the program only considers females, and 1:1 sex ratios typically occur in natural populations, the MVP estimates from the model must be doubled to include males. This correction was made for the values in Table 4.

Planning for Persistence

The MVP sizes resulting from the BOOMBUST model refer to geographically continuous populations of potentially interbreeding individuals. Such populations of *D. stephensi* can only be realized and sustained if reserves sufficiently large to support the recommended population size are protected. The observed population densities and the sizes of currently occupied sites, along with the selected MVP size, provide the basis for identifying areas in which protection of *D. stephensi* would best be focused.

Table 4. Initial population sizes needed to achieve various probabilities of persistence for different periods of time, according to BOOMBUST model results.

Probability of persistence	50 year	100 year	200 year
95%	5261	13,214	24,605
90%	2193	4798	8934
75%	833	1205	2094

Table 5. Minimum reserve sizes calculated for different minimum viable population (MVP) sizes and population densities.

MVP pop. size (duration, prob. of persistence)	Population density	Minimum reserve size	
	individuals/ha	ha	(acres)
24,600 (200 yr, $P = 95\%$)	50	492	(1230)
	10	2460	(6150)
	5	4920	(12,300)
13,210 (100 yr, $P = 95\%$)	50	264	(660)
	10	1320	(3300)
	5	2640	(6607)

Size of Reserves

The minimum reserve size for a single viable population of *D. stephensi* depends upon the selected MVP estimate and observed population densities of *D. stephensi* in the wild. Table 5 contains the minimum reserve size that would support various MVPs at three population densities ranging from low to extremely high for this species. Lower MVP values or higher population density values result in smaller minimum reserve areas, and vice versa (Table 5).

Because determination of reserve size depends directly upon estimated population density, we had to evaluate which among the range of observed densities is most reliable for determining habitat size. Observed densities in wild populations vary by over an order of magnitude from $\ll 5$ to about 60 individuals per ha (Thomas 1975, O'Farrell and Uptain 1989). Some of this variation is seasonal, correlated with the timing of reproduction and seasonal abundance of food. As discussed earlier, variation from year to year is probably dependent upon amount of rainfall. O'Farrell and Uptain's survey (1989) indicated that most of the currently occupied sites exhibit only trace ($\ll 5$ individuals/ha) or low (5 individuals/ha) abundance; areas of medium (5–10 individuals/ha) and high (> 10 individuals/ha) are uncommon. For the purposes of estimating critical reserve size for long-term persistence, we provisionally selected 10 individuals/ha as a reasonable intermediate value of average population density. Using 13,210 individuals as the MVP size (a population with 95% probability of persisting for at least 100 years), these values result in a critical reserve size of 1320 ha or 3300 acres (Table 5). Only one of the ten potential reserve sites proposed by consultants for the Riverside County Planning Department contains sufficient occupied habitat to meet this requirement (E.I.S. 1990).

The number of reserves is also an important issue. The geographic range of *D. stephensi* is unusually restricted for mammalian species, and variation in rainfall is correlated throughout its geographic range. Hence, drought is likely to stress simultaneously all populations throughout the range, although drought is less severe at higher elevations. The persistence of *D. stephensi* would best be served by several populations throughout its range (see also Price and Endo 1989), with one or more populations at higher elevations. A minimum of three viable populations, each in its own reserve, should safeguard persistence of the species against the chance extinction of a single population. Single populations, especially when small and isolated, are at risk from the effects of environmental, demographic,

and genetic stochasticity (Gilpin and Soulé 1986; Quinn and Hastings 1987). Even two populations are probably inadequate protection for this species, since environmental stress occurs in a correlated manner throughout the range (Price and Endo 1989). The presence of multiple populations reduces the risk that all would become extinct at the same time. Our consideration of currently occupied sites suggests that fewer than ten potential reserves exist.

Selection of Reserves

Protection of *D. stephensi* requires identification and preservation of suitable and potentially suitable reserves, as well as corridors between such sites. Corridors are important for both gene flow between populations and recolonization following a population crash. We ranked currently occupied sites in terms of feasibility of preservation and management—evaluating both the occupied area and the surrounding land. As did consultants for the Riverside County Planning Department (E.I.S. 1990), we considered the availability of habitat not known to be currently occupied, but apparently suitable for the species. Since the major threat to *D. stephensi* is habitat destruction through development, and many occupied sites are currently too small to sustain a viable population, we focused on the sites that could be enlarged or connected via corridors. Four variables were considered in the ranking of sites: (1) size of currently occupied site; (2) soil type of surrounding land; (3) status of land use of surrounding areas; and (4) to a lesser degree, site elevation.

(1) Size of Current Site. Our selected minimum reserve size is 1320 ha of suitable habitat, corresponding to a viable population of 13,210 individuals at an average population density of 10 individuals per ha. The sizes of currently occupied sites are from the site survey of O'Farrell and Uptain (1989). Most extant populations occupy areas of less than 400 ha, a size well below that of the minimum.

(2) Soil Types. Soil type is critical because habitat suitability is strongly influenced by soil characteristics (Price and Endo 1989). We generated a list of suitable soil types from the work of Price and Endo (1989) and O'Farrell and Uptain (1989); all other soil types were considered unsuitable. Using the Soil Survey of Western Riverside County Area (U.S. Soil Conservation Service 1971), we evaluated the areas surrounding sites occupied by *D. stephensi* for possible expansion of sites or provision for corridors between sites. The site was considered nonexpandable, if the area surrounding an occupied site was found to have "unsuitable" soils.

(3) Current Land Use. An equally important factor in determining habitat suitability is current land use. Based on information from the 1984 Upper Santa Ana River Drainage Area Land Use Survey and the 1986 San Diego Land Use Survey, we recognized four broad categories of land use: water storage, urban/residential, agricultural cropland, and native vegetation. Water storage (reservoirs) and urban/residential areas (including urban, suburban, rural residential, industrial, commercial, and some semi-agricultural uses) were considered inappropriate habitat for *D. stephensi.* Agricultural cropland included all field cropland, grazing land, orchards, vineyards, land used for incidental agricultural purposes, and idle agricultural land. Although not all agricultural land supports habitat for *D. stephensi* (e.g., deeply disked land is probably unsuitable), some kinds of agricultural land may support recolonization (O'Farrell pers. comm. 1989). Thus, any agri-

cultural land underlain by a suitable soil type was considered as potential habitat for *D. stephensi.* Areas of native vegetation were considered suitable if the underlying soils were suitable.

(4) Site Elevation. Elevation is a relevant consideration due to the potential for higher elevations to serve as refuges during times of drought.

We identified sites for potential reserves by integrating the results of the rainfall analyses, the demographic model, and information from maps of the area. We utilized maps at two scales. First, we mapped the distribution of extant populations of *D. stephensi* as reported by O'Farrell and Uptain (1989) on 7.5′ U.S. Geological Survey topographic maps at a scale of 1:24,000. Then we added the distribution of categories of land use for western Riverside County and the suitability of soil types in relevant areas. Selected information from the 7.5′ quadrangles was compiled on a base map and two overlays at a scale of 1:100,000, based on 30′ by 60′ U.S. Geological Survey topographic maps for San Bernardino, Santa Ana, Oceanside, Palm Springs, and Borrego Valley. The base map contained topography, rivers, reservoirs, and major highways. One overlay contained the occupied sites of *D. stephensi* from O'Farrell and Uptain (1989) (Fig. 1). The other overlay contained land use (Fig. 2).

On the 7.5′ quadrangles, we identified sites of currently adequate reserve size (1320 ha or greater) and sites capable of enlargement through expansion or connection by corridors to nearby occupied sites. Table 6 and Figure 10 summarize pertinent information about nine potential reserves. We ranked these sites as "critical," "high priority for evaluation," "low priority for evaluation," or "refuge." Critical habitats are those judged to be most valuable for protecting *D. stephensi* on the basis of current area, good potential for expansion or connection to other sites, and current abundance of *D. stephensi.* Of the two sites considered critical, the Warner Ranch in San Diego County (Figs. 1, 10) is especially important, because it is by far the largest currently occupied site (4548 ha; 11,370 acres), and probably contains the largest extant population of *D. stephensi.* Also, the Warner Ranch is at a higher elevation than most other sites (O'Farrell and Uptain 1987), thus providing habitat that is less likely to be stressed by droughts. "High priority for evaluation" refers to sites with currently or potentially adequate size or potential connection via corridors to adjacent sites. Such sites may include public land; encroachment from urban and agricultural development ranges from moderate to severe. "Low priority for evaluation" refers to sites which potentially provide appropriate habitat, but are currently too small and appear to entail more logistical difficulty to enlarge than "high priority" sites. "Refuge" refers to four small sites in the mountains of northeast Riverside County; each site is well below the critical habitat area. Although it is unlikely that these sites together could be enlarged to 1,320 ha, because they are at high elevation, they may support populations of *D. stephensi* during times of drought. Hence, these sites are considered important as protection against environmental stochasticity. These four sites are considered one potential refuge area.

We view the sites listed in Table 6 as core areas around which reserves should be designed. Since we were unable to evaluate the surrounding areas except as potential *D. stephensi* habitat based on soil type and land use, we do not recommend specific reserve boundaries and shapes. However, in their discussions of the design of reserves, Soulé and Simberloff (1986) and Diamond (1975) point

Table 6. Potential reserves for *D. stephensi,* based on integration of results from environmental analyses, the BOOMBUST model, and current distribution.

Site* no.	Current size (acres)**	Potential for expansion†	Potential for corridors†	Proximity of development	Rank
125	11,370	Good	?	Far	Critical
48	2310	Good	Good to 43 & 60	Close to W	Critical
24	2335	?	Good within 24	Close on perimeter	High priority for evaluation
96 + 97 + 98 + 110	?	Good	Good	?	High priority for evaluation
13 + 16	3830 (both)	Little	Good	Close	High priority for evaluation
82	1550	Good to SW	Possibly to 78	Close	High priority for evaluation
77 + 78 + 79 + 80 + 84 + 85	?	Fair	Good	Close	Low priority for evaluation
60	2184	Good to W	Good to 48	Close to E	Low priority for evaluation
26, 27, 28, 29	?	Fair	Poor	Far	Potential refuge

* All numbers refer to sites listed in O'Farrell and Uptain (1989) and Figure 2.
** From O'Farrell and Uptain (1989).
† Based on suitability of soils and adjacent land use (see text).

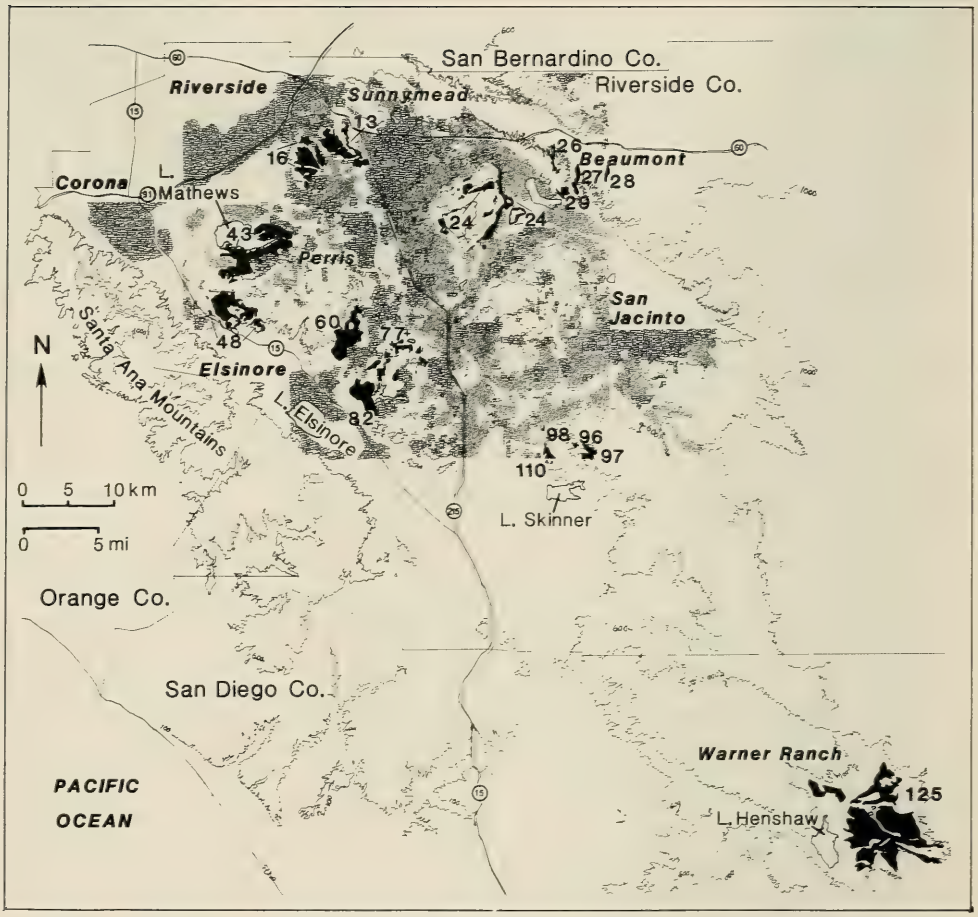

Fig. 10. Currently occupied sites that form the basis for nine potential reserves listed in Table 6. In most instances, sites would have to be expanded to meet minimum reserve size requirements.

out that all else being equal, reserve shape is optimized where boundary length is minimized. For example, for reserves of the same area, a round reserve is preferable to either square or extended linear shapes. Four of the reserves recommended by the E.I.S. (1990) (Alessandro Heights, Sycamore Canyon, Steele Peak, Mott Reserve) have long extended arms, and *D. stephensi* populations in these areas are in effect partially cut off from the main body of the reserve. The irregular reserve shapes promote a higher risk of extinction and lower probability of recolonization than if they were more circular.

Our proposed reserve sites are in close agreement with the sites recommended for preservation by O'Farrell and Uptain (1989). Unfortunately, comparisons between our results and the nine potential reserve sites proposed in the E.I.S. (1990) are difficult because they did not identify sites by the same names as did our common reference, O'Farrell and Uptain (1989). Hence, it is also difficult to evaluate the quantity of *D. stephensi* habitat in each of the proposed E.I.S. reserves. The largest and perhaps most important site we identified (Site 125, Warner Ranch), is in San Diego County and thus outside the review of the E.I.S. In

Riverside County, the core areas of most sites proposed by the E.I.S. appear to be the same areas we identified as important, although we combined O'Farrell and Uptain's sites differently. The E.I.S. does not provide biologically significant justification for the choice of lands surrounding their core areas; many of these apparently include habitat unsuitable for *D. stephensi.* In our recommendations, we combined sites and proposed connections between sites primarily with land that appears to be suitable habitat.

The E.I.S. also differs from our results in that they propose two areas, the "Potrero study area" and the "Santa Rosa study area" which we did not recognize as important reserve sites. O'Farrell and Uptain (1989) do not show any *D. stephensi* populations at the Potrero site, and while they do report that one of the two segments of the Santa Rosa site does have *D. stephensi* in low abundance, the eastern segment apparently does not.

All of our proposed potential reserves are based on the viable population size chosen from the results of the BOOMBUST model. Many smaller sites, not included here as potential reserves, may still be useful as refuges or sources of individuals for restocking or reintroduction. But without intensive management, populations of *D. stephensi* on these sites have a high probability of extinction.

Evaluation and Recommendations

Here we review the strengths and weaknesses of our approach, as well as recommended future activities which we feel are necessary for the persistence of *D. stephensi.* While acknowledging our limitations in evaluating the impact of environmental variables, in modeling populations, and in mapping the current and potential distribution of *D. stephensi* due to lack of available information, we point out that there is never "enough" information, especially for rare species. The following recommendations are therefore based on an analysis of the most accurate and current data available; we expect that revisions should be made in the conclusions and recommendations as new data are gathered. However, given the increasing encroachment of land development on *D. stephensi* habitat and the low population size of the species, recovery actions should be undertaken as soon as possible despite deficiencies in information.

Proposed recovery recommendations for *D. stephensi* are grouped into the basic categories of research and management, although many of the proposed activities overlap both categories. The research objective is to gather further information to evaluate the MVP analysis and minimum reserve size estimates, and to assess and select sites for reserves. Recommended management activities focus on acquiring and protecting adequate habitat, and appropriately managing this habitat—including the use of enhancement techniques where necessary.

Proposed Research Activities: Refine the Population Simulation Model

The BOOMBUST model is tailored to the life history characteristics of *D. stephensi,* and is particularly useful in incorporating important aspects of environmental stochasticity such as rainfall. However, the BOOMBUST model does not accurately simulate the behavior of very small populations, particularly in their high potential for extinction due to random genetic or demographic fluctuations. Thus, the model is likely to overestimate the probability of survival for all *D. stephensi* populations, as nearly all iterations experienced population bot-

tlenecks during random recurrent runs of low rainfall. Also, we assumed that rainfall patterns over the next 50, 100, or 200 years will be similar to those of the last century. Many predictions of future global and continental rainfall patterns differ substantially from present patterns (e.g., Schneider 1989).

While the correlation between rainfall and rodent population fluctuations appears clear, the estimation of how rainfall influences both fecundity and survivorship is based on weaker data. For example, we could have estimated average litter size in *D. stephensi* as 1.3 female offspring per litter, according to Lackey (1967b). This number is based on the production of 16 newborns produced by six wild-caught females. Lackey does not report the size or sex ratio of any individual litters, and there are not other data available for *D. stephensi.* However, this litter size is somewhat low compared to that reported in closely related species. We instead used 1.7 as the average, based on the much larger sample size reported by Zeng and Brown (1987). Similar caveats should be made concerning most of the other life history parameters used. Our estimations of how these parameters covary with rainfall are considerably less well supported. Perhaps the clearest indication that the assumptions used in the model are acceptable is that the model results are consistent with those of long-term field studies such as that of Zeng and Brown (1987). However, additional life history data would be invaluable in refining population simulation, and confidence in the model's predictions could be strengthened by detailed monitoring of natural *D. stephensi* populations.

Proposed Research Activities: Assess and Select Proposed Recovery Sites

Another major research problem is the status of detailed information on the distribution and abundance of this species. In addressing this lack of information, we have been invaluably aided by maps provided by O'Farrell and co-workers. However, these maps include an acknowledged level of uncertainty; in some cases, large areas of known or potential habitat could not be sampled thoroughly. Additionally, researchers debate the accuracy of different methods used to determine the presence or abundance of *D. stephensi,* particularly to distinguish the burrows of *D. stephensi* from those of similar species (Price pers. comm. 1989). Even where use of burrows as an index is well-established, observed burrows can only be used as indices of presence because it is unclear how many burrows an individual regularly uses. Furthermore, standard trapping techniques may lead to overestimates of population fluctuations due to variation in trapping success. For example, lunar phase has been shown to affect trapping success of other small rodents (Munger et al. 1983; Price et al. 1984). Also, according to O'Farrell (pers. comm. 1989), *D. stephensi* are less prone to enter traps during seasons of abundant food. Thus, most of the currently used census methods have a high uncertainty.

In most cases the land use maps we used to identify possible reserve sites were several years old, and the situation regarding remaining habitat has almost certainly worsened in recent years. Many of the recommended reserve sites depend on the existence of corridors among sites. Evaluation in the field will determine which of the recommended sites in Table 6 can be enlarged, connected to other sites, or improved as adequate habitat.

A field survey should be carried out immediately to confirm and expand upon the information presented in O'Farrell and Uptain (1989), in order to evaluate

the proposed reserve sites. This evaluation should determine the extent of occupied habitat, habitat type and quality, *D. stephensi* abundance, land use, and potential threats to the sites. The type and quality of surrounding habitats should be assessed for potential corridors or expansion of small populations. Important habitat characteristics include: type of dominant vegetation, extent of shrub cover, density of grass cover, soil types, prevalence of steep slopes or escarpments, other barriers to dispersal, signs of use by *D. stephensi,* disturbances, present land use, and encroachment by adjacent land uses. In addition, detailed information should be gathered from county records and landowners on land ownership and the susceptibility of each site to urban or agricultural conversion. A geographic information system (GIS) would be particularly useful for this task.

Based on this review, the capability of proposed recovery sites to provide the appropriate quantity and quality of habitat could be better assessed, as could the feasibility of protecting and maintaining such habitat. Suitable sites could then be prioritized based on their importance to the long-term persistence of *D. stephensi,* the political and logistical feasibility of designating the site as a reserve, and the degree of threat to the site. Immediate protective actions could then be focused on top-ranked sites.

Other relevant research topics which would facilitate the management of *D. stephensi* populations include research on the optimum corridor design, the type of disturbance mechanisms required to maintain appropriate grassland habitat, and reintroduction techniques to be employed if necessary to restore populations that go extinct.

Proposed Management Activities: Protect Critical Habitat

Encroachment by land development and fragmentation of remaining habitat parcels pose a major threat to remaining *D. stephensi* populations. Immediate management activities must focus on acquiring and protecting enough suitable habitat to ensure the long-term persistence of *D. stephensi.* Following the assessment of the proposed recovery sites listed in Table 6, an appropriate number of sites should be acquired, protected, and managed based upon minimum habitat size estimates. Dispersal corridors should be established between populations wherever feasible.

Options for the protection of recovery sites must be identified; such determinations may largely depend on whether designated sites are on public or private property. Several proposed sites lie on federal (Bureau of Land Management) and other publicly owned land. Where possible, lands containing established *D. stephensi* populations that are already owned by governmental agencies and private conservation groups should be used as reserve sites. Interagency cooperation should be promoted in order to achieve adequate protection of these sites. However, much *D. stephensi* habitat is privately owned. Wherever possible, important privately owned habitat should be acquired and placed under management authority of the Fish and Wildlife Service or private non-governmental organizations through outright land purchase, purchase or donation of development rights, conservation easements, or by governmental agencies trading unsuitable lands for suitable lands. Where land acquisition is not feasible, managers are urged to establish appropriate management contracts or develop management strategies

with private landowners. Given the accelerated rate of land development in southern California, the political feasibility of setting aside essential habitat will have to be taken into account when selecting recovery sites.

Proposed Management Activities: Develop and Implement Management Plans

Specific management plans should be developed and implemented for each population. Since management may involve city, county, state, and federal agencies, we propose the establishment of a permanent interagency task group to minimize conflicts and facilitate the implementation of management plans (see Clark and Westrum 1989). Each plan should establish a management regime that will maintain annual grasslands containing:

1) a maximum of 30% vegetative cover (this percentage may be exceeded in the wet season);
2) a grass–forb ratio as close to 1:1 as possible, but not to exceed 50:1 on more than one third of the reserve (see O'Farrell and Uptain 1987, Table 2);
3) minimal woody vegetation; and
4) a disturbance mechanism, such as fire, grazing, and/or shallow disking (based on future research findings), to maintain appropriate grassland habitat.

Specific management techniques could be developed and employed, when necessary, to enhance the survival of *D. stephensi* within recovery areas. During summers of high moisture stress, as indicated by preceding March rainfall levels, food provisioning may prove useful in preventing large population declines. Additionally, techniques for reintroduction should be investigated and tested, to be employed in the event that a reserve population goes extinct.

Population sizes on each reserve should be monitored using standardized techniques and time of year. Density of active burrows may be the most efficient index, given that live-trapping is not reliable at all times of the year.

Negative human impacts on and surrounding reserve lands need to be closely controlled. The rapid growth in population and development in Riverside County accounts for much of the disturbance to *D. stephensi* habitat. Access into *D. stephensi* reserves by feral and domestic animals should be minimized. Also, any activity, such as off-road vehicle use, which has deleterious effects on *D. stephensi* habitat should be prohibited within reserves.

Any attempts to maintain self-sustaining populations of *D. stephensi* will be greatly enhanced by thorough enforcement of federal and state laws protecting the species and its habitat. Such efforts may be aided by initiatives to increase public awareness and support for recovery efforts, both to change behavior that undermines *D. stephensi* recovery, as well as to encourage citizens to ensure that the necessary management activities are carried out. Potential techniques include: press releases, exhibits, public speakers, educational programs, media coverage of any events (e.g., lectures, land purchase ceremonies, site visits, etc.), and workshops. Educational efforts might best be targeted at groups having direct impacts on *D. stephensi* populations: e.g., farmers could be taught how *D. stephensi* would benefit from changes in farming practices, private landowners (especially of large holdings) taught how to manage land for *D. stephensi,* and developers and planning agencies made aware of the need for open space within rapidly developing areas.

Conclusion

This study has developed estimates of the minimum viable population (MVP) size for the endangered species *Dipodomys stephensi* (Stephens' kangaroo rat). These estimates were the basis for identification of possible reserves that could support such populations within its geographic range.

Dipodomys stephensi is a granivorous, heteromyid rodent, limited in distribution to an arid region in southern California. In arid environments, variability in rainfall is often high and rodent populations fluctuate markedly. These fluctuations increase the chance of extinction at the low period of the population cycle. Within the range of *D. stephensi,* rodent abundance is positively correlated with early spring rainfall. We found high climatic covariation among sites throughout most of the range of *D. stephensi,* indicating that drought is likely to stress all of the range at once. Nevertheless, average differences in precipitation between some sites are significant, so sites at higher elevation may be beneficial as refuges during droughts.

The BOOMBUST model was designed to simulate population growth for species that undergo substantial, periodic fluctuations in population size in relation to a dominant environmental parameter. The model utilized information and assumptions about survivorship and fecundity of *D. stephensi* in relation to rainfall, as well as stochastic variation in rainfall based on historical climatic records. The predicted MVP sizes (Table 4), which we consider minimal, are large compared with previous estimates of population sizes that would provide for the long-term persistence of this species (e.g., Price and Endo 1989). The MVP estimates are large because of the demographic characteristics of *D. stephensi,* the dependence of population size on rainfall, and the probability of recurrent drought as based on historic climatic data. The MVP sizes are so large that relatively few currently occupied sites could potentially sustain a viable population at an intermediate population density (10 individuals/ha), at the selected probability of persistence (95%) and persistence time (100 years).

Based on the MVP estimates and maps of current distribution, land use, and soil types, we suggested nine potential reserves (Table 6 and Fig. 10) for evaluation in the field. We recommend that at least three viable populations of *D. stephensi* be established within its current geographic range. Of the nine suggested reserves, several factors argue strongly for the Warner Ranch in particular as an extremely important potential reserve. Further study of changes in land use and the abundance of *D. stephensi* since the mid-1980s should clarify which additional areas are feasible as reserves. Price and Endo (1989) recommended placing reserves as far apart as possible and over heterogeneous but suitable habitat, because fluctuations in rainfall are correlated throughout the species' range. We concur and recommend that some sites at high elevation, such as those in the mountains near Beaumont, be established to serve as refuges during drought.

Areas chosen as reserves may need periodic management of vegetation for this species and occasional enhancement through provisioning during times of drought. Since March rainfall patterns can be used to estimate recruitment of *D. stephensi* later in the year, managers can anticipate and prepare for drought.

Additional information would refine both the predictions of the BOOMBUST model and recommendations for management. Further documentation of the

demography and ecology of *D. stephensi* would improve the reliability of MVP estimates. Updated evaluations of current habitat, current abundance, and land use would clarify which of the proposed reserves are ecologically as well as logistically appropriate.

This study of *D. stephensi* illustrates more general issues as well. Through most of its range, the persistence of *D. stephensi* is in conflict with urban and agricultural development—a dilemma that faces an ever-growing number of species around the world. Resolution of this conflict requires not only the kind of population viability analysis presented here, but also decisions by society about our coexistence with other species. The MVP sizes reported here suggest that *D. stephensi* is at the brink of extinction. With large enough reserves, the species will probably persist; without them, it will probably disappear within the next hundred years. Finally, this species is but one of many endangered species from the arid ecosystem of the southwestern United States (see Table 1). Since many other endangered and threatened species occur within the historic range of *D. stephensi,* the proposed reserves would benefit not just this species but also the associated desert community.

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